Force and EMG signal patterns during repeated bouts of concentric or eccentric muscle actions

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Healthy males ($n = 14$) performed three bouts of 32 unilateral, maximal voluntary
concentric (CON) or eccentric (ECC) quadriceps muscle actions on separate days.
Surface electromyography (EMG) of the m. vastus lateralis (VL) and m. rectus femoris
(RF) and torque were measured. Integrated EMG (IEMG), mean (MPF) and median
power frequencies and torque were averaged for seven separate blocks of four
consecutive muscle actions. Torque was greater ($P < 0.05$) for ECC than for CON
muscle actions at the start of exercise. It did not decline throughout ECC exercise, but
decreased ($P < 0.05$) markedly for each bout and over bouts of CON exercise. Thus,
torque overall was substantially greater ($P < 0.05$) for ECC than for CON exercise. At
the start of exercise IEMG of VL or RF was greater ($P < 0.05$) for CON than for ECC
muscle actions. This was also true for overall IEMG activity during exercise. The
IEMG increased ($P < 0.05$) modestly for both muscles during each bout of CON or
ECC muscle actions, but did not change for the VL over bouts. The IEMG of RF
decreased ($P < 0.05$) modestly over CON but not ECC exercise bouts. At the beginning
of the first bout of exercise the IEMG/torque ratio was twofold greater ($P < 0.05$) for
CON than ECC muscle actions. The ratio of IEMG/torque increased ($P < 0.05$)
markedly during CON but did not change during ECC exercise. Thus, by the end of
the third bout there was a fivefold difference ($P < 0.05$). The MPF decreased
($P < 0.05$) substantially in each CON bout with only a partial recovery between bouts. In
contrast, MPF remained the same within each bout and over bouts of ECC exercise.
These results indicate that the ability to maintain force during repeated bouts of
maximal voluntary muscle actions at a relatively high angular velocity is remarkably
greater for eccentric than for concentric exercise. It is suggested that the factors
responsible for fatigue and for changes in the EMG signal pattern during concentric
exercise do not materialize during, or are different for, eccentric exercise as performed
here.

Key words: localized muscular fatigue, mean power frequency, motor unit recruitment,
power density spectrum.

Muscle fatigue or failure of muscle contractile
components is mainifested in increased

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electromyographic (EMG) activity relative to
force. Numerous studies show that EMG am-
plitude increases when isometric force at
15-70% of maximum voluntary is sustained
until failure (Cobb & Forbes 1923, Lippold *et al.*
1960, Viitasalo & Komi 1977). Fatigue under

these conditions appears to be of mainly peripheral origin (cf. Asmussen 1979, Edwards 1981). These changes are associated with a decrease in the mean or median power frequency of the EMG signal (cf. Basmajian & DeLuca 1985). This occurs due to an increase in the low-frequency (Kogi & Hakamada 1962) and a decrease in the high-frequency regions of the power spectrum (Kaiser & Petersén 1963, Kadefors *et al.* 1968). To a lesser extent changes in force and the EMG signal pattern have been examined during dynamic exercise. During consecutive maximum voluntary concentric (CON) muscle actions, force declines markedly, the mean power frequency decreases and the EMG/force ratio increases (Komi & Tesch 1979).

Force development during muscle lengthening contributes substantially to normal locomotory activity (Cavagna *et al.* 1964). Eccentric (ECC) muscle actions, in addition, have frequently been reported to result in delayed muscle soreness and compromised force output (cf. Komi & Viitasalo 1977, Armstrong, 1984, Sargeant & Dolan 1987, Kroon & Naejie 1988). Surprisingly, therefore, information describing the force and EMG responses to ECC muscle actions is scarce (Komi & Rusko 1974, Komi & Viitasalo 1977, Komi *et al.* 1987). Maximum force at a given angular velocity or joint angle is always greater during maximum voluntary ECC than CON muscle actions (Asmussen 1953, Doss & Karpovich 1965, Komi & Buskirk 1972, Komi & Rusko 1974, Olson *et al.* 1972). This difference is potentiated by involuntary activation (Gravel *et al.* 1987, Triolo *et al.* 1987). Thus, the inherent ability of isolated skeletal muscle to develop greater force when lengthening than when shortening at a given speed is dependent on the method of activation (Flitney & Hirst 1969, Joyce *et al.* 1969). It follows that the integrated EMG (IEMG) for a given tension output has been found to greater for CON than for ECC muscle actions (Bigland-Ritchie & Woods 1976, Basmajian & De Luca 1985, Moritani *et al.* 1988). Recently, different motor unit recruitment (Nardone & Schieppati 1988, Nardone *et al.* 1989) and different fatigue patterns (Gray & Chandler 1989) have been reported for these distinct types of muscle actions. These observations, when taken together, suggest that the EMG/force relationship and power spectrum density function of the EMG signal should differ depending on whether CON or ECC muscle actions are performed.

This study compared torque, IEMG and the power spectrum density function of the EMG during the performance of repeated bouts of consecutive, maximum voluntary CON or ECC muscle actions. An exercise regimen that has been shown to produce marked reductions in force for CON quadriceps muscle actions was employed (Colliander *et al.* 1988). This response and the alterations in the EMG signal pattern found previously for CON muscle actions (Komi & Tesch 1979) occurred in the present study. In frank contrast, no force decline and minimal changes in the EMG signal were found for ECC muscle actions. The results were interpreted to suggest that either the factors responsible for mechanical failure are fundamentally different for ECC versus CON muscle actions or they are the same but were not manifest for ECC exercise in this study.

MATERIALS AND METHODS

Fourteen males, with no history of cardiovascular or orthopaedic pathologies, volunteered for this study. Their mean (SE) age, height and weight were 33 (2) years, 176 (2) cm and 81 (3) kg. Their maximal oxygen uptake during treadmill running was 40.5 (1.9) ml kg^{-1} min^{-1}. After being informed of the protocol and procedures of this study, which were approved by the Human Research Review Committee of the Kennedy Space Center, each gave written consent.

Once each week for the 4 weeks prior to the start of the study, subjects were accustomed in standarized sessions to the isokinetic loading dynamometer (Kin/Com, Chattecx Corp., Chattanooga, TN, USA) and testing protocol (see below). After calibration of the dynamometer to the manufacturer's specifications, subjects were seated in the dynamometer chair and stabilized using thigh, hip and chest straps. The input axis of the dynamometer was aligned with the axis of rotation of the knee joint and the ankle strapped to the lever arm. The alignment was duplicated for repeated tests by recording length of lever arm, elevation of dynamometer head, and table, platform and seat positions for each subject.

Subjects were examined on two separate days. On each, two maximum isometric muscle actions separated by 1 min of rest were performed with the lever arm 45° below horizontal. Force was rapidly increased from 50 N and the effort maintained for 2–3 s. Maximal voluntary isometric torque was defined as the highest 1-s average during the 'plateau'. The two values on each day of testing were averaged to

determine each subject's maximal voluntary isometric torque. These values did not differ ($P < 0.05$) for days 1 and 2 of testing (224 ± 14 and 221 ± 14 N m respectively). The test–retest reliability was $r = 0.96$ ($P < 0.001$).

After the isometric efforts, three bouts of 32 maximal, voluntary unilateral CON or ECC quadriceps muscle actions were performed. Multiple bouts were used in an effort to allow expression of the factors responsible for muscle failure during ECC muscle actions. We knew that a single bout of ECC actions like those used in this study caused minimal fatigue (Gray & Chandler 1989). A large number of consecutive muscle actions was not performed because of the extreme difficulty in doing so, especially during maximal voluntary CON efforts (Tesch 1980). The torque that had to be overcome to initiate movement of the lever arm was set at zero. Muscle actions were carried out at a constant angular velocity ($180°$ s^{-1}) and at a rate of approximately 1 s^{-1}. Each bout was followed by 60 s rest with the limb 40–$70°$ below horizontal. The CON and ECC muscle actions were performed through an 80 to $10°$ and a 10 to $80°$ range of motion respectively. Encouraged by the examiner, subjects were instructed to perform muscle actions with maximal effort through the entire range of motion. Visual feedback was always provided by displaying the force curves on a computer monitor. The CON exercise was performed 2 days before ECC exercise because CON muscular activity preceding ECC does not impair ECC exercise performance (Jones *et al.* 1986, Colliander & Tesch 1987).

The EMG signals were measured using two Ag–Ag/Cl surface miniature electrodes (2 mm diameter; Sensormedics Corp., Anaheim, CA, USA) separated by 20 mm. These were positioned for m. vastus lateralis (VL) about 15 cm proximal to the basis patella along a line from the patella to the trochanter major and for m. rectus femoris (RF) about 20 cm proximal to the basis patella along a line from the patella to the iliac crest. Reference electrodes (15 mm diameter, Sensormedics Corp.) were applied to the contralateral VL. The electrode positions were marked with ink to assure standardized measurements from day to day.

The EMG signals from VL and RF were amplified 500 times and recorded onto FM tape (TEAC Corp., Japan) with low and high cut-off frequencies of 1.5 and 2300 Hz respectively. These were subsequently reamplified 10 times and refiltered between 7.5 and 2300 Hz to increase digitizing accuracy and to reduce limb motion artifact. The refiltered EMG signal was used for IEMG and frequency analysis. Dynamometer arm position (DAP) was extracted from the dynamometer circuitry and recorded on FM tape. Gravity-compensated torque and DAP were also digitized in real time using an IBM-compatible computer. The IEMG, mean power frequency (MPF) and median

power frequency (MDPF) for VL and RF were calculated.

For IEMG analyses the EMG signals were full-wave rectified and passed through a smoothing window with a time constant of 47 ms. Using the DAP, the IEMG and torque were averaged over an angle-specific window (24–$61°$ below horizontal) for each of the 32 CON or ECC muscle actions. The first two and the last two muscle actions were omitted due to incomplete activation or missing data. The IEMG and torque for four consecutive muscle actions were subsequently averaged.

For the maximal isometric muscle actions, the highest 1-s average of IEMG during the 'plateau' in torque was considered maximal voluntary isometric IEMG. For each subject the two values for each day of testing were averaged. The maximal voluntary isometric IEMG for each muscle on days 1 and 2 of testing were similar (371 ± 36 vs 411 ± 41 μV for VL; 264 ± 27 vs 319 ± 33 μV for RF), but not strongly related (VL: $r = 0.68$, $P < 0.01$; RF: $r = 0.59$, $P < 0.02$). Because maximal voluntary isometric torque on days 1 and 2 of testing were similar and showed less variation, the day-to-day variability in the IEMG was due to differences in electrode application rather than alterations in the inherent IEMG/force relation (Viitasalo & Komi 1975). Accordingly, each subject's IEMG values for ECC exercise (day 2) were multiplied by the ratio of day 1 to day 2 maximal voluntary isometric IEMG to control for variability in sensoring.

For frequency analyses DAP was used to trigger acquisition of 1024 points from both VL and RF refiltered signals. With the limb moving at $180°$ s^{-1} the sample rate was increased from a typical 1 kHz to 5 kHz to limit the data acquisition to the segment of each muscle action where constant angular velocity was maintained. This was the same angle-specific window used for IEMG analysis (24–$61°$ below horizontal). The data for each muscle action were then passed through a Hamming window and converted to their power spectrum using fast Fourier transform (FFT) by means of commercially available software (DSP, Cambridge, MA, USA) which invoked a mixed radix FFT. Again, from the original 32 muscle actions the first two and the last two muscle actions were omitted. On the remaining 28 muscle actions the spectra from four consecutive actions were averaged providing seven spectra to be used for final analyses. The MPF and MDPF of these seven spectra were subsequently calculated. Therefore, the seven data points (see Figs. 1–4) presented represent muscle actions 3–6, 7–10, 11–14, 15–18, 19–22, 23–26 and 27–30.

Values are given as mean and standard error (SE). A two-way ANOVA was applied to establish changes within a bout or over bouts and between CON and ECC conditions. The IEMG data were analysed by
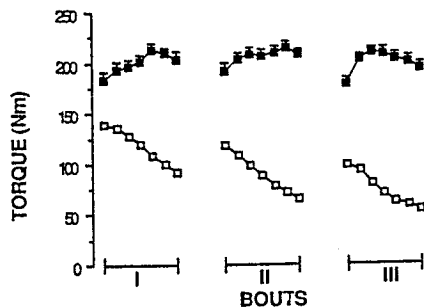
Fig. 1. Torque for three bouts (I, II or III) of CON (□) or ECC (■) muscle actions. Each data point represents the average of four consecutive muscle actions. Values are mean ± SE. The SE bars are within the symbols for CON exercise.

using the differences between the ECC or CON IEMG and their respective IEMG for the maximal voluntary isometric muscle action for each subject. Statistical significance was set at $P < 0.05$.

RESULTS

Torque output was greater ($P < 0.05$) for ECC than CON muscle actions at the start and throughout exercise. Torque decreased (34–47%, $P < 0.05$) almost linearly for each CON bout. Likewise, there was a decrease ($P < 0.05$) in peak (muscle actions 3–6) and average (muscle actions 3–30) torque over the three CON bouts. In contrast, torque increased ($P < 0.05$) modestly within each bout but did not change over bouts of ECC exercise. Accordingly, the difference in torque output between ECC and CON exercise became progressively greater ($P < 0.05$) over bouts (Fig. 1).

The overall IEMG for VL and RF was greater ($P < 0.05$) for CON than for ECC exercise (Fig. 2). This was also true for each muscle at the start of exercise. For the VL for each type of muscle action the IEMG did not change over bouts. Likewise, the RF showed no change in IEMG activity over bouts of ECC muscle actions. This muscle did, however, show a modest reduction ($P < 0.05$) in the IEMG over bouts of CON muscle actions. Both muscles showed a modest increase ($P < 0.05$) in the IEMG during each exercise bout independent of muscle action type (Fig. 2).

The IEMG/torque ratio during CON muscle actions increased ($P < 0.05$) throughout any bout (Fig. 3). In contrast the IEMG/torque
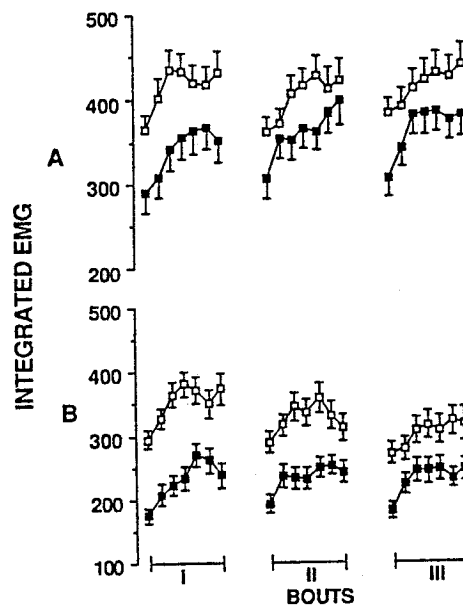

Fig. 2. Integrated EMG (IEMG) for m. vastus lateralis (A) and m. rectus femoris (B) during CON (□) and ECC (■) exercise. Values for ECC were corrected for sensoring variability (see Methods). For further details see Fig. 1.

ratio for ECC exercise did not change. At the beginning of exercise the IEMG/torque ratio was twofold greater ($P < 0.05$) during CON than during ECC muscle actions. This difference became greater ($P < 0.05$) during each bout. By the end of the third bout the IEMG/torque ratio was fivefold greater ($P < 0.05$) for CON than for ECC muscle actions (Fig. 3). These IEMG/torque data reflect the average of the
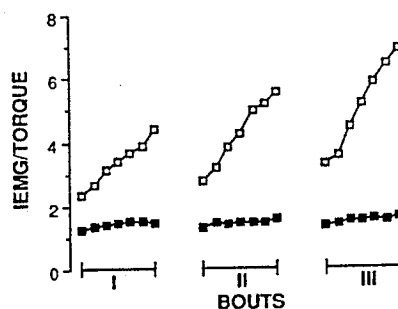

Fig. 3. IEMG/torque ratio during CON (□) and ECC (■) exercise. IEMG for m. vastus lateralis and m. rectus femoris was averaged. Values for ECC were corrected for sensoring variability (see Methods). For further details see Fig. 1.
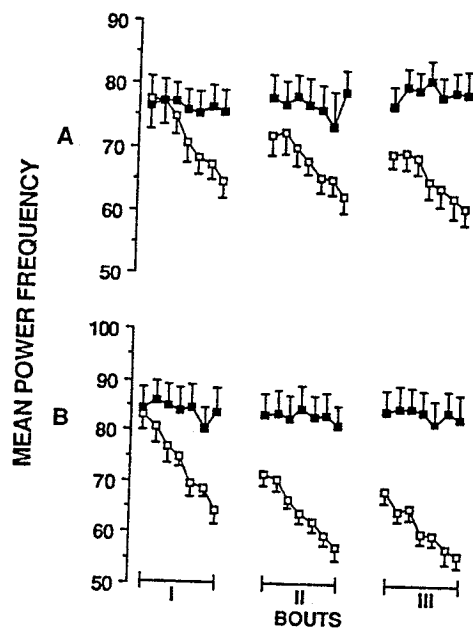
Fig. 4. Mean power frequency (Hz) during CON (□) and ECC (■) exercise for m. vastus lateralis (A) and m. rectus femoris (B). For further details see Fig. 1.

IEMG activity of the VL and RF. Similar results were obtained if the IEMG of either muscle was used in calculating the IEMG/torque ratio.

The MPF at the beginning of exercise was similar for the VL and RF. The MPF of the VL or RF decreased ($P < 0.05$) in each bout and over bouts of CON muscle actions. However, it remained the same for the VL or RF within each bout and over bouts of ECC exercise (Fig. 4). Because overall changes in MDPF paralleled those of MPF and MPF showed less fluctuation between blocks of muscle actions, we have chosen to report MPF data only.

DISCUSSION

This study showed a difference in fatigue responses between repeated bouts of CON and ECC muscle actions performed at a relatively high angular speed. During repeated CON muscle actions force decayed. Similar results obtained under almost identical experimental conditions have been reported (Nilsson *et al.* 1977, Komi & Tesch 1979, Colliander *et al.* 1988). The force loss was not paralleled by a concomitant decrease in IEMG. This agrees

with the findings of others (Nilsson *et al.* 1977). In contrast, there was minimal decrease in force and no change in IEMG over repeated bouts of high-speed ECC muscle actions. No decline of force during a single bout of ECC muscle actions performed at the same velocity used in the present study has recently been reported (Gray & Chandler 1989). As a consequence of these responses the IEMG/torque ratio increased multifold during CON exercise but remained essentially unchanged during ECC exercise. Moreover, the MPF of the EMG decreased during each bout and over bouts of CON muscle actions, but showed little or no change for ECC exercise. These results, taken together, suggest almost no central or peripheral fatigue during repeated ECC muscle actions. In frank opposition to this performance of maximal CON muscle actions resulted in marked force loss, mainly because of contractile failure.

Apparently contradictory to these findings, force loss was greater during the performance of ECC than CON muscle actions of the elbow flexors (Komi & Rusko 1974) or knee extensors (Komi & Viitasalo 1977). The IEMG decreased slightly and to a similar extent for the two exercise modes. In comparing these results to those of the present study, it should be appreciated that substantially more rest was allowed (10-fold) between consecutive muscle actions and the muscle action velocity was lower in their work. This may have accounted for the smaller relative force and IEMG reductions they observed during CON muscle actions than noticed here. We have reported a similar decrease in force to theirs which was paralleled by a decrease in IEMG when CON muscle actions were performed at a relatively slow speed (Tesch *et al.* 1983).

The minimal fatigue found in the present study for fast-speed ECC actions as compared to the appreciable fatigue for slow-speed ECC actions reported by Komi and co-workers (Komi & Rusko 1974, Komi & Viitasalo 1977) probably occurred because efficiency increases with the speed of this type of muscle action (Komi *et al.* 1987). In the light of the fact that force is similar for fast- and slow-speed maximal voluntary ECC actions of the knee extensors (Westing *et al.* 1988, Dudley *et al.* 1989), the metabolic demand would be expected to be smaller for fast- than for slow-speed ECC actions. Moreover, rotation of recruitment among motor units and thus greater

sharing of the resistance to stretch may be greater for fast- than for slow-speed ECC actions. The torque–velocity relationship of the knee extensors with maximal voluntary ECC efforts shows that force is not greater. than during isometric actions (Westing et al. 1988). When ECC actions are evoked in situ by artificial means, however, the relationship is comparable to that of isolated muscle (Hather et al. 1989).

Motor unit recruitment patterns during ECC and CON muscle actions have not been extensively studied. Force production at a given angular speed, however, is much greater during lengthening than during shortening of muscle (Asmussen 1953, Doss & Karpovich 1965, Komi & Buskirk 1972, Olsson et al. 1972, Komi & Rusko 1974). This does not necessarily imply that more motor units are brought into play because maximum IEMG for voluntary ECC and CON muscle actions is similar or only slightly higher during ECC muscle actions performed at slow speeds (Komi & Buskirk 1972, Komi & Viitasalo 1977). The results of this study, examining muscle actions of higher speed, imply a different pattern. Thus, overall IEMG activity was greater for CON than for ECC exercise. This was also true for the VL or RF at the start of exercise. This finding is in accord with that of Komi et al. (1987) showing greater EMG activity during CON than during ECC muscle actions performed at high angular velocities. Likewise, for a given submaximal tension, knee extensors or arm flexors show higher EMG activity during shortening than during lengthening (Bigland-Ritchie & Woods 1976, Basmajian & DeLuca 1985, Moritani et al. 1988).

The neural input required to produce a given force is much lower during ECC than during CON exercise in the non-fatigued state. Likewise, when neural input is the same for ECC and CON muscle actions, force is much greater for the ECC condition. Accordingly, the 'additional' force during ECC exercise must be generated by mechanisms other than recruitment or frequency modulation. It is generally believed that the contribution of elastic components of the muscle tissue to force production is substantial during ECC exercise even in the absence of reflex potentiation mechanisms (Cordo & Rymer 1982). This is indicative of greater mechanical efficiency during ECC tension development due to storage of elastic energy in the actin–myosin cross-

bridges that enables each individual sarcomere to develop greater tension when being forcibly stretched than when allowed to shorten (Huxley & Simmons 1971).

Recent reports suggest marked inhibition of force production during maximal voluntary ECC muscle actions (Gravel et al. 1987). Similarly, in response to electrical stimulation paralysed muscles showed a greater difference in force between CON and ECC muscle actions than typically seen in intact human muscle (Triolo et al. 1987). From these studies maximum ECC torque at relatively slow speeds appears to be twofold greater than maximum CON torque. However, maximum voluntary force is reported to be only 30–40 % higher for ECC than for CON muscle actions (Asmussen 1953, Doss & Karpovich 1965, Olsson et al. 1972, Komi & Buskirk 1972, Komi & Rusko 1974). Consequently, the entire motor unit pool does not appear to be fully activated during maximal, voluntary ECC muscle actions even though force is slightly greater for ECC than for CON exercise under these conditions.

The fact that IEMG and torque increased in parallel at the beginning of each ECC bout in the present study suggests an inability to recruit the entire motor unit pool. Reduced neural drive was most evident at the beginning of the third bout. Force and IEMG were depressed despite no evidence of fatigue at the end of the preceding bout. At the beginning of the third bout force and IEMG increased in parallel. The MPF, however, did not change. The apparent increase in neural drive with no change in MPF implies that additional motor units were recruited. It therefore appears that, despite maximal voluntary effort and greater force, the entire motor unit pool is not fully activated during ECC muscle actions. This or the possibility of rotation among motor units may at least in part explain the lack of fatigue during ECC exercise. In support of this, derecruitment of slow motor units and selective recruitment of fast-twitch motor units have been suggested to occur during voluntary ECC muscle actions (Nardone & Schieppati 1988, Nardone et al. 1989).

Analyses of the power spectrum of the EMG signal have been used extensively to ascertain muscle fatigue. An increase in the low-frequency (Kogi & Hakamada 1962) and a decrease in the high-frequency regions (Kaiser & Petersén 1963, Kadefors et al. 1968) of the EMG power

spectrum accompany voluntary force loss. As a consequence, the MPF or MDPF of the EMG signal decreases (cf. Basmajian & DeLuca 1985). This frequency shift has consistently been demonstrated during sustained isometric actions of constant force (Stulen & DeLuca 1981), maximal isometric muscle actions (cf. Bigland–Ritchie 1981) or repeated maximal dynamic muscle actions performed at various speeds (Komi & Tesch 1979, Tesch *et al.* 1983).

The MPF is highly correlated with muscle fibre conduction velocity (Sadoyama *et al.* 1983). Accordingly, a decrease in conduction velocity which is caused by exercise-induced acidosis is mainly responsible for the decrease in MPF during muscular activity (Lindström *et al.* 1970, Mortimer *et al.* 1970, Stulen & DeLuca 1981). Alternatively, although supportive data are limited, changes in motor unit recruitment or synchronization of motor units have been proposed to alter MPF (cf. Basmajian & DeLuca 1985, Arendt-Nielsen *et al.* 1989).

Muscle fibre conduction velocity increases in response to increased muscle temperature (e.g. Arendt-Nielsen *et al.* 1989). Moreover, ECC exercise is associated with markedly higher muscle temperatures than CON exercise when both are performed at a comparable power output, rate of oxygen uptake or heat production (Nadel *et al.* 1972, Nielsen *et al.* 1972, Pahud *et al.* 1980). It can therefore not be excluded that the differences in MPF found in the present study between ECC and CON exercise partly reflect a temperature-dependent influence on conduction velocity. A decreased conduction velocity due to metabolic changes resulting in lowered muscle pH (Stålberg 1966) could therefore have been masked. Nevertheless, the EMG frequency spectrum does not shift during repeated bouts of ECC muscle actions, at least when these are performed at high rate and speed. Accordingly, it appears that neither muscle conduction velocity nor motor unit recruitment changes substantially in response to ECC exercise.

The peripheral fatigue typically noticed during CON exercise is most likely due to depressed actin–myosin cross-bridge formation. Hydrogen ions have been suggested to interfere with calcium ions for binding sites at the troponin level (Nakamura & Schwartz 1972, Robertson & Kerrick 1979). Previous studies that have used protocols similar to that of the present study

show substantial accumulation of lactate in muscle (Tesch *et al.* 1978, Jansson *et al.* 1987, Tesch *et al.* 1989). The pH has been estimated to be 6.5 or less (Sahlin 1978). Likewise, there is a marked decrease in the ATP/ADP ratio (Jansson *et al.* 1987) and creatine phosphate decreases to one-third of basal levels with only partial recovery between bouts (Tesch *et al.* 1989). These changes may in a large part explain the reduced mechanical force output and the concomitant frequency shift that occurred in response to a single bout or repeated bouts of CON exercise.

If fast-twitch motor units are preferentially recruited during ECC muscle actions (see above), it may seem different to reconcile the greater fatigue found during CON than during ECC exercise in the present study. Fast-twitch motor units are more susceptible to fatigue and have less ability to recovery than slow-twitch motor units (cf. Edwards 1981, Basmajian & DeLuca 1985). These patterns have been demonstrated indirectly during voluntary CON exercise using the protocol employed here (Nilsson *et al.* 1977, Komi & Tesch 1979, Colliander *et al.* 1988). Individuals with a preponderance of fast-twitch muscle fibres showed greater force loss and less recovery than individuals with a high percentage of slow-twitch muscle fibres. However, it should be appreciated that mechanical efficiency is markedly greater for ECC than for CON exercise (Bigland-Ritchie & Woods 1976, Komi *et al.* 1987). Thus, skeletal muscle should experience less metabolic demand during and more rapid recovery from ECC exercise. Therefore, changes in the energy state of muscle that interfere with membrane excitation and force development were probably less during ECC than during CON exercise. However, the results of the present study could also be explained if the factors that are responsible for fatigue are fundamentally different between CON and ECC exercise.

In conclusion, these results provide evidence of different fatigue responses to repeated bouts of CON and ECC muscle actions. The pronounced force decay observed during CON exercise was not paralleled by a corresponding decrease in neural drive. In contrast, neither force nor IEMG changed over bouts of repeated ECC exercise. The MPF decreased in response to CON, but not ECC, exercise. Therefore, changes in motor unit recruitment or muscle

fibre conduction velocity must have been substantial during CON exercise but negligible during ECC exercise.

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